THE AUTOTOMY OF THE HYDRANTH OF TUBULARIA.

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When colonies of *Tubularia crocea* are brought into the laboratory, and placed in aquaria, they sooner or later lose their hydranths. The hydranths become pinched off from the stems and fall to the bottom of the aquaria where they disintegrate. Later, new hydranths are regenerated in place of the old ones.

Somewhat similar cases of the loss of the hydranth have been reported by various workers on other species. All such instances, however, involve an absorption of the hydranth, preceded by a dissolution of the body through histolysis. *Tubularia,* alone, is known to pinch off its hydranths completely from the stems before extensive histolysis occurs or indeed, any whatsoever.

Loeb[1] found in a species of *Campanularia,* an absorption of the hydranth when the individual came into contact with the sides of the dish or with any other solid object. Thacher[2] corroborated Loeb so far as an absorption occurred, but no evidence of any effect of contact in producing the action could be determined. Loeb also reported absorption in two other genera, viz., *Margelis* and *Antennularia,* where, however, the inciting cause was believed by Loeb to be the changes the stems underwent under the action of gravity. No one has studied this special feature in these forms since Loeb. As will be spoken of later, *Tubularia* does not show any such response.

Thacher (*l. c.*) described absorption in two species of *Eudendrium, E. ramosum* and *E. tenue,* and also in *Pennaria tiarella. Pennaria carolinii,* an allied species, was studied by

[1] Loeb, J., "The Transformation and Regeneration of Organs," *Amer. Journ. Phys.,* Vol. 4, 1900.

[2] Thacher, H. F., "Absorption of the Hydranth in Hydroid Polyps," BIOL. BULL., Vol. 5, p. 297.

Cerfontaine[1] and by Gast and Godlewski.[2] Cerfontaine believed that the cause of the absorption lay in the difficulty with which the fully formed hydranth responded to sudden changes in its environment, whereas the regenerated ones are better adapted by " une acclimation rapide."

Gast and Godlewski (*l. c.*) have examined the case more critically. They show that, at the beginning of the process, the tentacles are withdrawn until nothing is left externally to show where they once existed. The peristome likewise disappears and the mouth closes. Ultimately, all that is left of the hydranth is a small smooth knob. This, too, becomes absorbed into the stem and a cicatrix alone remains. Then regeneration may begin. Concomitant with these external changes, the cells of the endoderm begin to dissociate and disintegrate and come to lie as detritus in the lumen of the hydranth. The current flows down into the stem and carries the débris and this continues until the whole of the hydranth has been absorbed. The changes in the cells are not restricted to the endoderm cells for those of the ectoderm lose their vacuoles and become greatly reduced in size. They remain, however, much longer *in situ* than the cells of the endoderm. The changes seem to affect, from the first, all of the cells of the hydranth and the process is only in this sense a local one. Moreover, inasmuch as open communication between the hydranth and the rest of the stem is maintained, it cannot be urged that the process is a passive one, due simply to the death of the cells of the hydranth. In this respect, the description of Gast and Godlewski is similar to that to be given for *Tubularia*.

The first evidence of autotomy in *Tubularia* is the sinking of the hydranth upon the stem. This pendent position results from a constriction of the cœnosarc at the base of the hydranth, where it joins the stem. For a time the hydranth hangs suspended by the perisarc, but soon this breaks and the hydranth falls. During the whole of this process, including, generally, the first half hour

[1] Cerfontaine, P., " Recherches experimentale sur la regeneration et l'heteromorphose chez astroides calycularis et *Pennaria carolinii*," *Arch. de Biol.*, t. 19, 1902.

[2] Gast, R., und Godlewski, E., Jr., " Über den Regulationserscheinungen bei *Pennaria carolinii*," *Arch. für Entwickelungsmec.*, Bd. 16, 1903.

while the hydranth lies at the bottom of the dish, completely severed from the stem, the tentacles are seen to move about as in a normal individual. After a longer or shorter time, varying with external conditions, the movements cease, the hydranth becomes whitish and evidences of disintegration become apparent. The cœnosarc of the stem, on being freed from the hydranth, early shows a collection of red pigment, described by Driesch, Loeb, Stevens and Morgan in their studies of regeneration in this genus. The tube of the stem has been closed distally by the folding and compression of the walls even before the hydranth has been lost. For a time immediately after the autotomy of the hydranth has taken place, the cœnosarc withdraws for one of two millimeters down the perisarc tube, leaving free, ragged edges to the outer tube projecting beyond the protoplasmic portions. Soon, however, the cœnosarc is seen to be flush with the top of the perisarc.

Sections through hydranths and stems at the period when the hydranth is falling, show a constriction of the protoplasmic parts immediately beneath the attachment of the hydranth to the stem. The perisarc seems to take no active part in the changes involved in autotomy. The walls of the cœnosarc, involving both ectoderm and entoderm, are folded upon themselves. In some specimens there seems to be an indication of histolysis setting in among the cells forming the ectoderm and entoderm in the portion of the cœnosarc tube involved in the constriction. When it occurs, such dissociation of the cells is of local occurrence only and is to be found only in the constriction. Examination of the hydranth in such cases (Fig. 1), shows it to be perfectly normal as far as one may judge from histological evidence. Moreover, living specimens, as has been mentioned, show activity of the tentacles even after the hydranth has been removed.

For a time, varying with the individual, the hydranth remains attached to the stem by the perisarc only and it is the weight, probably, of the hydranth which ruptures the chitinous perisarc and frees the hydranth from the stem. One may see, in the individuals at this stage, resting in the aquaria, that all protoplasmic attachment has been withdrawn and longitudinal sections

bear this out. At the base of the hydranth and at the distal end of the stem, from which the hydranth has been severed, there is no definite arrangement of the cells into ectoderm and entoderm. The cells seem to lie freely in the chitinous envelop. The

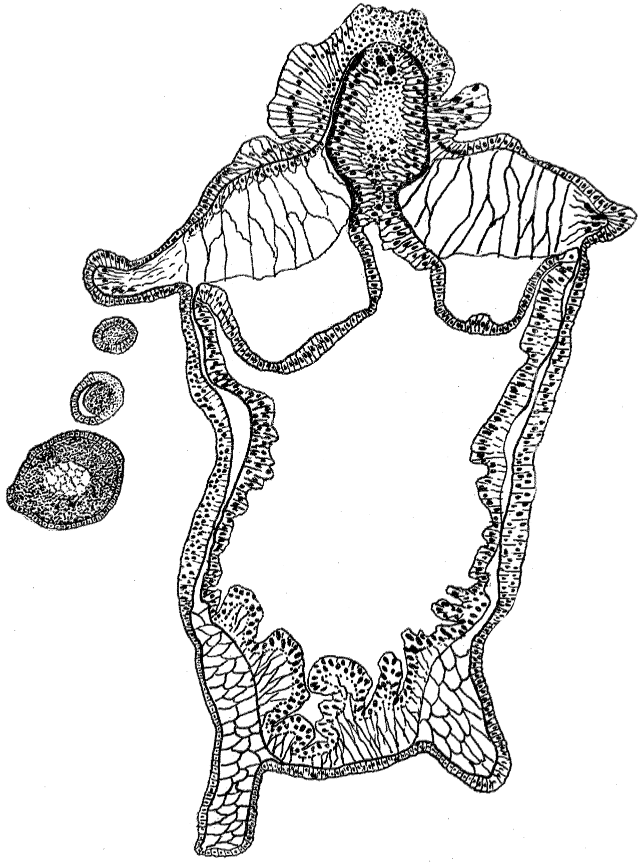

FIG. 1. Sagittal section of *Tubularia* hydranth immediately after autotomy. The hydranth had fallen to the bottom of the dish.

cylindrical or flattened epithelium cells of ectoderm and entoderm of the normal individual have now assumed a spherical form. In the iron-alum stain, the nuclei appear for a time normal, but later distinct changes, undoubtedly pathological, have set in. There is no indication of an absorption of such cells into the lower portions of the stems as Gast and Godlewski (*l. c.*) have described for *Pennaria*.

The process of disintegration of the cells of the hydranth which has been cut off from the stem, is ushered in by dissociation of the cells of the entoderm (Fig. 2). There is no constancy in location of the origin of this process, but, in the main, it seems to set in at the proximal end, *i. e.,* at the end formerly connected with the stem. The entoderm cells leave their positions around the periphery of the hydranth, immediately beneath the ectoderm and come to fill the whole of the cavity of the hydranth. This cavity, at the same time, begins to become smaller in volume. Then, after a time, the ectoderm cells begin to participate in the process of dissolution. The gonanths are

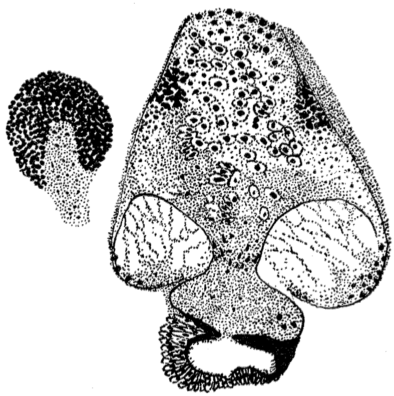

FIG. 2. Hydranth which has begun to disintegrate, in sagittal section. A gonanth is shown also in section; the cells are normal.

the last to suffer (see Fig. 2). Even after the hydranth has begun to lose its shape, as it lies at the bottom of the dish, these reproductive bodies show little histolysis.

In order to determine what factors were operative in causing autotomy, the writer performed a series of experiments on *Tubularia.* The following external factors were considered: (1) Temperature effects—(*a*) heat, (*b*) cold; (2) light, involving its absence, darkness; (3) gravity; (4) aëration; (5) mechanical factors, such as abrasion, force of current, etc.

1. *Temperature.* (*a*) *Effects of Heat.*—A fingerbowl, containing a dozen stems of *Tubularia* fresh from the sea, was placed in the direct sunlight, where the temperature registered

25° C. A control was placed in the shadow near it.[1] Within half an hour evidences of autotomy became apparent and within one and one half hours, over half of the hydranths had been lost. In the control, where the temperature of the water registered 5 degrees lower (25° C.), the hydranths were retained for half a day. More striking still was the rapidity of autotomy in the case of the fingerbowl of specimens placed in an apartment immediately over the boilers of the engine-room of the Bureau of Fisheries Laboratory where the temperature is constantly at 33° C. In this case all of the hydranths had fallen entirely from the stems within two hours, while a few had fallen within one hour.

(*b*) *Cold Effects.*—A fingerbowl of specimens, 12 in number, was placed in an ice-chest at a temperature of 8° C. The hydranths in this case were retained for three weeks and undoubtedly would have persisted had not the experiment been terminated accidentally. The specimens were examined from day to day and they gave every indication of being normal, inasmuch as the tentacles were active at all times. Food was provided for the hydroids, but it was not possible to determine whether they fed or not. In another set of experiments, specimens were kept a week at a temperature of 10° C. in a fingerbowl resting in chipped ice, the bowl being placed in diffuse light. At the end of the week, the individuals were apparently healthy and no indication of autotomy could be determined.

It cannot be urged against these experiments that the animals became benumbed and their activities thereby lessened with consequent retention of the hydranths, for as we have seen, they were aparently normal and active throughout.

2. *Effect of Sunlight.*—In the experiments with the effects of light, it was necessary to insure against heat effects. Various methods were used for obviating this factor. A large vessel, with a volume of about six gallons, was provided with a platform which rested about ten centimeters from the bottom of the vessel and fifteen from the surface of the water over it. On this platform, a fingerbowl of *Tubularia* stems was placed. Then

[1] The possibility of light being the factor here is considered later.

the larger vessel was filled with water so that the fingerbowl was submerged to a depth of fifteen centimeters. The apparatus was placed in the direct sunlight, which fell upon it from eight o'clock in the morning until about four thirty in the afternoon. The temperature of the water was kept at 20° C. It was not possible to reduce the temperature of the water, under the circumstances, below this. Control specimens were placed in a similar vessel, somewhat smaller, in the shadow near the larger one. The first hydranths fell from the individuals in the larger vessel, exposed to the rays of the sun, during the third day. Those in the control gave evidence of autotomy at about the same time, or even earlier, perhaps. This result is quite similar to that given by colonies of *Tubularia* brought into the laboratory and placed in running salt water either in the light or in the dark. It seems to point to the absence of any effect of sunlight in inducing the process of autotomy. The hydranths very probably would have remained longer if the temperature could have been reduced, as is shown in other experiments to be described.

In another set of experiments fingerbowls of specimens were placed in a trough of chipped ice and set in the direct sunlight. The hydranths were retained for nearly two weeks. In a third set, under more natural conditions, stems of the hydroid were tied to weighted blocks of wood and these were submerged about fifteen centimeters beneath the surface of the water in the " outer pool " of the Bureau of Fisheries at Woods Hole, where the tide sweeps through at all times, bringing cool water from Vineyard Sound and Buzzards Bay. The individuals, of course, were subjected to the direct rays of the sun. The hydranths were retained for two weeks and this would have continued undoubtedly if the waves during a stormy period had not torn the specimens from their supports. The average daily temperature of the surface water during this time of year was 19° C. At night the temperature fell to 15° C.

We may conclude from these experiments that sunlight is not a factor in producing autotomy in *Tubularia*.

With respect to darkness, data have been given already to show that this is not a potent factor. In the case of hydranths placed in the ice-chest, the individuals were not exposed to light

for more than a few moments during the day. Therefore, if the absence of illumination was a positive factor in inducing the process of autotomy, it most assuredly would have been made evident here. In another case, specimens were attached to weighted blocks of wood, as used in an earlier experiment, the block being covered with a tin case. These were lowered beneath a bridge over a tide-way to a depth of two fathoms. The individuals were therefore in almost total darkness. The temperature of the water at this depth was lower than that of the surface, owing to tide currents. The hydranths were retained for over two weeks, when the experiment was terminated.

3. Stems of *Tubularia* were tied to supports in running water of a temperature of about 20° C. The supports could be so arranged that the stems were inclined at any angle with respect to gravity. The hydranths were cut off by autotomy in three days at whatever angle the stems were placed. Inasmuch as this time corresponds to that in which the hydroids of colonies introduced into aquaria from the sea, lose their hydranths and since no decrease in the time of autotomy could be determined, to be correlated with the position of the hydroid with respect to gravity, the writer does not believe that this factor is operative in autotomy. Loeb, it will be recalled (*l. c.*), believed that gravity induced absorption in *Antennularia*. This case of Loeb's is the only one recorded in which gravity acts. When one recalls the fact that the stems of *Tubularia* are placed in any position with respect to the vertical in their natural habitat on rocks and piles, it would seem quite extraordinary that such effects of gravity should obtain in this species. Moreover, in strong currents, such as the tide which sweeps over the rocks of the Tide-mill at South Harpswell, Maine, the stems are subjected to a force which causes incessant change in their axes with respect to gravity.

4. To determine the effect of lack of oxygen, a liter of sea water was boiled for half an hour and cooled to 20° C. in an hermetically sealed vessel. Specimens of *Tubularia* were put into the water and the vessel, now exposed to the air, was placed in the ice-chest. Within two hours nearly every hydranth had fallen from the stems.

In another set of experiments, excess of oxygen was supplied by means of the Mast aërating device. The vessel containing the hydroid stems was placed in chipped ice and the aërating apparatus delivered bubbles of air to one corner of the dish. However, here, no lengthening of the period of retention of the hydranths could be determined when the temperature was permitted to rise to ordinary room temperature (21° C.). Therefore, while lack of oxygen causes autotomy to set in, an excess of the gas over and above that which forms normally the oxygen content of sea water at these temperatures does not prolong the period of retention of the hydranths; they behave as if they had been brought in from the sea and placed in an ordinary aquarium under ordinary conditions.

It will be recalled that the specimens in the fingerbowls which were kept in the ice-chest were not supplied with air artificially. Moreover, the water was not changed, so that the air which was over the surface of the water of the bowls was sufficient to supply the oxygen needed by the animals. The oxygen content of water kept under such conditions cannot vary to any great degree and the sea water, flowing over the animals in their natural habitats varies, as has been determined, comparatively little in the amount of air in solution. Moreover, the specimens which, on being introduced into the laboratory lose their hydranths, are kept, in the main, supplied with ever changing water in which the oxygen content is practically that of the surrounding sea, or even higher, owing to the condensation by the pumps. Therefore this factor cannot be of any considerable importance in causing autotomy.

5. Considerations were given to mechanical effects such as the swaying of hydranths on the stems in a strong current of water, rubbing of the stems against one another and mechanical shock induced by cutting off the hydranths from the stems.

With respect to the first factor, we know that in nature, in many cases, *Tubularia* grows where tide causes whirlpools and an ever changing direction in the currents passing over the hydroids and therefore, one would not look for this as a cause of autotomy. Experiments were performed to show that the factor is not operative, by placing stems, bearing healthy

hydranths in jets of water which caused an incessant waving of the hydranth on the stem. The hydranths were retained, under such conditions, as long as was compatible with the temperature and other external conditions. Abrasion was likewise made the question of another set of experiments and here, too, no effect could be correlated with the factor. With respect to mechanical shock, when the stems are removed from the colonies, data have already been given, for in the ice-chest experiments, where the hydranths were retained for a long time, the stems had been cut from the colony. Moreover, in those specimens which were placed on floats in the sea and where the hydranths did not fall off, the individuals had been cut from the stems. Therefore, mere cutting of the stems is not a factor in autotomy.

It will be seen that temperature seems to be the only consistent factor involved in the decapitation. When the temperature is kept at about 10° C. or 15° C., the hydranths are retained, regardless of any other factors with the one exception of lack of oxygen, which we believe to be inoperative except under wholly artificial conditions. When it is recalled that in the sea, *Tubularia* may be found throughout the summer[1] in latitudes where the temperature of the water does not rise above 18° C. or 20° C., while in lower latitudes[2] the occurrence of this species on the piles and rocks is correlated with the times of the year, spring and fall, when the water is cooler, we find sufficient data from natural sources to conclude that temperature is the potent factor in causing autotomy of the hydranths in colonies brought into the laboratory.

The case of *Hydra,* described by Greely[3] where the body becomes reduced to a mass of dissociated cells when the temperature is reduced to 4° C. and 6° C., seems to weigh against the present conclusions, but more recently Caroline McGill[4] has

[1] As at South Harpswell, Maine, where the temperature of the water seldom rises above 16° C.

[2] *E. g.,* Woods Hole, Mass. *Tubularia* disappears when the temperature of the water reaches 20° C. It reappears again for a time in the fall.

[3] Greely, "Further Studies on the Effects of Variations of Temperature on Animal Tissues," Scientific Papers.

[4] McGill, C., "The Effect of Low Temperature on *Hydra,*" BIOL. BULL., Vol. 14, 78.

studied the histological changes occurring in *Hydra* subjected to reduced temperatures and is unable to corroborate Greely, but rather shows that a loss of water accompanies the lowering of the temperature, which causes the hydroids to become opaque, without degenerative changes in the cells.

Little success has been had with *Tubularia* in exhibition tanks. If some means could be devised for keeping the water in such tanks at a temperature, say of 15° C., the writer believes that *Tubularia* could be maintained in health, as in the sea.

The writer has studied *Tubularia* at the Bureau of Fisheries and the Marine Biological Laboratory, at Woods Hole and at the Harpswell Laboratory. To those in charge of these laboratories, Professors Sumner, Lillie and Neal and to Dr. Kingsley and Professor Lambert, the writer is indebted for much kindness. The work was started at the suggestion of Dr. T. H. Morgan and the writer is grateful to him for generous aid and criticism.

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